

Sustainable monitoring of roe deer in public hunting areas in the Spanish Pyrenees

J. Herrero¹, R. T. Torres^{2*}, C. Prada³, A. Garcia-Serrano³,
A. Gimenez-Anaya³ and O. Fernandez⁴

¹ Area of Ecology. Technical School of Huesca. University of Zaragoza. 22718 Huesca, Spain

² CESAM & Department of Biology. University of Aveiro. Campus de Santiago. 3810-193 Aveiro, Spain

³ Ega Wildlife Consultants. Sierra de Vicort 31. 50003 Zaragoza, Spain

⁴ Pyrenean Institute for Ecology (CSIC). P.O. Box 64. 22700 Jaca, Spain

Abstract

Aim of study: Monitoring trends in animal populations is essential for the development of appropriate wildlife management strategies.

Area of study: The area is situated in the southern Pyrenees (Aragon), Spain.

Material and methods: To measure the abundance, population trends, sex ratio, and mortality of roe deer populations, we analyzed data from i) driven hunts for wild boar (hunting seasons 1995/96-2009/10, n = 1,417, ii) itineraries, which were used to calculate the KAI and density using DS (2003-2010, n = 310 itineraries), iii) roe deer carcass recoveries (2006-2010, n = 100), and iv) data from the deer hunting quota fulfillment (2006-2010, n = 325 hunted animals).

Main results: Based on DS, in 2010, the average density of roe deer populations was 2.3 km⁻² (CV 17%). Based on the KAI and the battues, the estimated average annual rate of increase was 5.8% and 4.3%, respectively. Based on the KAI and the carcass recoveries, the estimates of the population sex ratio were 0.75 (n = 641) and 0.9 (n = 100) males per female, respectively. Carcass recoveries indicated that mortality was highest in late winter and early spring. The average body masses and sizes of males and females were within the ranges reported for other Iberian and European populations.

Research highlights: Monitoring should be continued in the Aragon population of roe deer, although larger sample sizes are required to increase the accuracy of estimates and assessments of the impact of management actions.

Key words: *Capreolus capreolus*; hunting bag; distance sampling; KAI; Spain; rangers; long-term monitoring.

Introduction

In Europe, populations of large herbivores have increased their size and distribution (Gill, 1990), which have been favored by socioeconomic changes in rural areas (Apollonio *et al.*, 2010). The management of sustainable populations of wild ungulate depends on the monitoring of the status of populations and the detection of trends (*e.g.*, Gordon *et al.*, 2004), and an accurate evaluation of a population is fundamental to proper management planning and decision-making (Buckland *et al.*, 1993). Many techniques have been used to monitor such ungulate populations (see review by Mayle *et al.*, 1999) and to estimate absolute densities (Apollonio *et al.*, 2010). Generally, the

methods used depend on the specific objectives of the study, the management questions to be addressed, the behaviour of the species and, especially, the effort that can be applied to the fieldwork. Monitoring populations is essential to improve the understanding of ecological processes, particularly of expansion (Acevedo *et al.*, 2005) or inter-specific competition (Focardi *et al.*, 2006), for implementation of epidemiological surveys (Acevedo *et al.*, 2007) and in general terms, for the development of appropriate management strategies (Putman *et al.*, 2011).

On the Iberian Peninsula and, particularly, in Spain, the number and distribution of roe deer —*Capreolus capreolus*— have increased dramatically. In the Aragon region, in the middle of the 19th Century, roe deer were

* Corresponding author: rita.torres@ua.pt.

Received: 26-02-12. Accepted: 29-06-13.

limited largely to a few areas in the Pyrenees; however, in the last 30 yr, the distribution of the species has increased rapidly (Gortázar *et al.*, 2000; Osuna *et al.*, 2006). Despite the cultural and economic significance of this species, little attention has been paid to the populations of the Pyrenees (Leránz and Castién, 1996; Cargnelutti *et al.*, 2002; Marco *et al.*, 2011) and there is a shortage of information on the demographics of these populations, even though they are hunted heavily. In 1995, roe deer populations began to be monitored in the Pyrenean Game Reserves of Aragon based on driven hunts for wild boar *Sus scrofa* (battues) (Jędrzejewska *et al.*, 1994, 1997). Since 2003, we have monitored roe deer populations in those areas using itineraries, which were used to calculate Kilometric Abundance Index (KAI, Vincent *et al.*, 1991) and absolute density, adapting the Distance Sampling procedure (Buckland *et al.*, 1993). In 2006, roe deer hunting was permitted in the Game Reserves following a Game Management Plan (Prada *et al.*, 2007) and,

thereafter, hunting quota fulfilments were recorded and biometric data were taken from harvested animals.

We report population density, structure, mortality, and trends in the roe deer population in the Aragonese Pyrenees based on 7 years of monitoring. Based on the results we have identified recommendations for modifying the Management Plan for the Hunting Reserves that can improve the accuracy of population estimates.

Material and methods

Study area

The study area was in a 127,099 ha portion of the Aragonese Pyrenees, and comprised a variety of public areas that are managed by the government of Aragon. The study area ($42^{\circ} 42' 42''$ N, $0^{\circ} 5' 35''$ W) consists

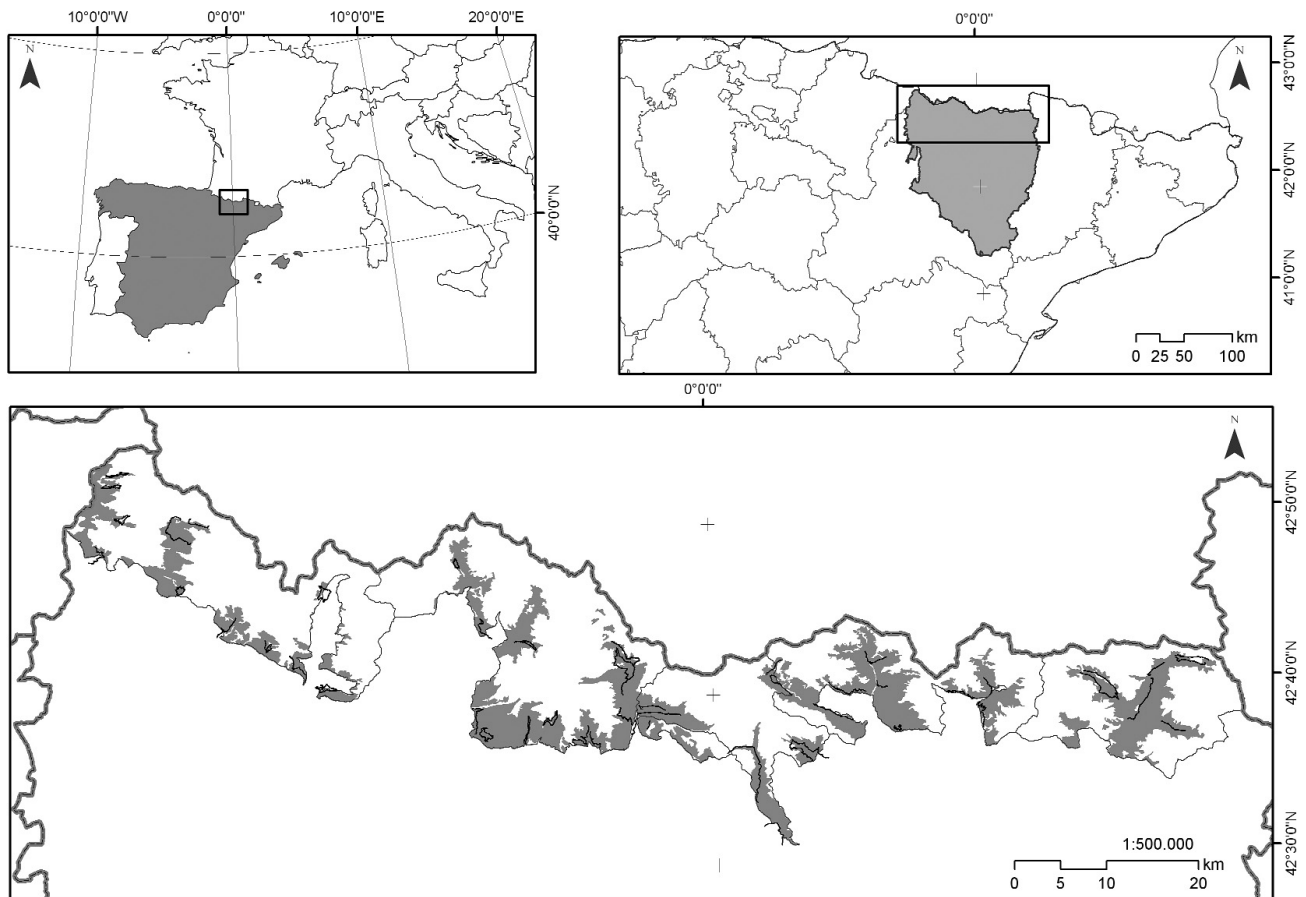


Figure 1. Location of the study area in the Spanish Pyrenees.

of mountains, with elevations ranging from 600 m to 3,404 m. Most of the vegetation communities are within the Eurosiberian domain. At high elevations (>2,200 m), low alpine grasslands predominate. Between 1,600-2,200 m, the predominant forest species are Scots pine *Pinus sylvestris*, mountain pine *Pinus uncinata*, and beech *Fagus sylvatica*, although large tracts have been transformed by human activity into scrubland and alpine grasslands. Other wild ungulates in the area are the Pyrenean chamois *Rupicapra p. pyrenaica* and wild boar, both of which are hunted, and there are some red deer *Cervus elaphus*. In addition, red fox *Vulpes vulpes* is present. The economy is mainly based on tourism and livestock. The human population density is 8.8 persons km⁻². Hunting is performed using battues (wild boar) or stalking (Pyrenean chamois and roe deer), and rangers accompany the hunters.

Population density and trends

Itineraries for KAI and distance sampling

We established 53 itineraries (mean length = 4.8 km, SD = 1.7) that followed footpaths and covered 256 km. The itineraries were chosen systematically to provide complete coverage of the study area, and, using a fine-scale map of the estate and aerial photographs, and then were digitalized. From 2003 to 2010, sampling was performed in early spring (April and May). By doing so, we avoided the period when the ground is covered by snow and the slopes are difficult to traverse. A strict protocol for the fieldwork was designed and followed: itineraries were walked slowly and in silence by one or two trained rangers after dawn (when roe deer are the most active) when visibility was good (no precipitation, fog, or strong winds). On average, each itinerary lasted 170 min. Each observer was equipped with binoculars, *ad hoc* maps, and datasheets. Itineraries were used to calculate the KAI (relative density index) and absolute density based on Distance Sampling (Buckland *et al.*, 1993). When a single or a group of roe deer was detected, the observer(s) estimated the distance from the itinerary to the animal(s). In addition, the following parameters were recorded: sex and age class (*i.e.*, adult male, adult female, juvenile) (when possible), which provided the basis for calculating basic demographic parameters:

sex ratio (males *per* females) and productivity (kids *per* female). Other variables (time of day, habitat, and distance to the observer) were also recorded. Distance Sampling 6.0 software (Thomas *et al.*, 2010) was used for the analyses. Population density, the detection function, and the average cluster size of the deer groups were estimated. The data were right-truncated to exclude the 5% most distant observations (Buckland *et al.*, 2001). Half-normal, uniform, and hazard rate models for the detection function were fitted to the data using cosine, hermite polynomial, and simple polynomial adjustment terms, which were fitted sequentially. For the density estimates, we regressed ln (cluster size) on detection probability, but used mean cluster size if the regression was non-significant at $p = 0.15$. The best model and adjustment term were chosen based on Akaike's Information Criterion (AIC), a low coefficient of variation (CV), a low number of parameters, and a non-significant χ^2 .

Battues

The battue, a traditional hunting method that is used in the area to hunt wild boar entails having a hunter wait for the game species to be driven toward them by beaters and their hunting dogs. The procedure flushes the wild boar and other animals (*e.g.* roe deer) and they pass in front of stalls, where observers can record the number of individuals. Between the 1995/1996 and 2009/2010 hunting seasons, rangers collected data and the density estimates were based on the number of roe deer observed during the battues and the area covered by the driven hunt; however, this method provides a subestimation of the overall density (Jędrzejewska *et al.*, 1994, 1997). For that method to be effective it is essential to know the area covered by the battues; therefore, each of the battue areas were digitally mapped using GIS at a scale of 1:10,000. To calculate roe deer density, each battue was assumed an independent sampling unit and, therefore, by analysing the data by hunting area or year, we could calculate the average density of each hunting area or time (Herrero, 2003).

Mortality

To estimate the natural mortality of roe deer, beginning in 2006, bi-monthly, rangers recorded animals that were found dead. They recorded the sex of the animal and the apparent cause of death.

Biometry

Beginning in 2006, all of the roe deer killed by hunters were weighed (Pesola®) and the following measures taken: longitudinal head-body length, height at the withers, and chest girth.

Results

Between 2003 and 2010, 310 itineraries were performed and 1,083 roe deer were observed. Average group size was 1.5 (95% CI = 1.48 – 1.6, $n = 641$) and did not differ significantly between years (Median test $\chi^2 = 11.9$, d.f. = 7, $p = 0.10$). The sex ratio was 0.75 males *per* female ($n = 641$).

Population density and trends

KAI

KAI varied between 0.53 and 0.93 roe deer *per* km (2003-2010) (Table 1), and the number of roe deer *per*

km increased significantly ($R^2 = 0.62$; $p = 0.02$) with an average annual increase of 5.8% (2003-2010).

Distance sampling

Distance Sampling (2003-2010) indicated that the density of roe deer ranged from 1.6 to 3.9 roe deer km^{-2} (VC 17-35%), which represents 595 – 1,481 roe deer (Table 2), but density did not change significantly over time (all of the 95% confident intervals overlapped).

Battues

The sizes of the areas covered by the battues were highly variable (2.6 ha to 778.3 ha); therefore, the analysis was limited to the hunting areas that were between 50 ha and 250 ha (hunting season: 1995/96 to 2009/2010, $n = 1,417$). Roe deer densities ranged between 0.8 km^{-2} and 1.9 km^{-2} and increased significantly at a rate of 4.3% ($R^2 = 0.51$, $p = 0.003$).

Table 1. Itineraries conducted to monitor roe deer in the Game Reserves in Aragon, Spain (2003-2010)

	Itineraries	Effort Km	Roe deer observed	Roe deer listened	Roe detected	KIA	N Cluster	Males	Females	SR
2003	41	192	106	9	115	0.60	80	42	46	0.91
2004	39	181	115	11	126	0.70	74	43	58	0.74
2005	20	143	67	9	76	0.53	43	25	32	0.78
2006	41	193	129	0	129	0.67	85	29	60	0.48
2007	42	196	126	7	133	0.68	81	36	59	0.61
2008	42	199	148	20	168	0.84	99	59	70	0.84
2009	42	197	122	23	145	0.74	73	43	54	0.80
2010	43	205	175	16	191	0.93	106	67	82	0.82
Total	310	1,506	988	95	1,083	0.72	641	344	461	0.75

Table 2. Density of roe deer in the Game Reserves of the Aragonese Pyrenees (2003-2010)

	Itineraries	Effort Km	Clusters	Cluster average	D	D lcl	D ucl	D CV	GOF Chi-p	Function	N	N lcl	N ucl
2003	41	192	79	1.33	3.7	2.1	6.4	29	0.24	HZ_SP T250	1384	795	2,409
2004	39	181	72	1.55	3.3	2.3	5.0	21	0.02	UN_cos T250	1259	852	1,859
2005	20	143	43	1.56	2.4	1.4	4.1	26	0.13	UN_cos T250	853	511	1,421
2006	41	193	68	1.52	3.9	2.0	7.7	35	0.04	HZ_sp T10%	1481	753	2911
2007	42	196	80	1.56	2.4	1.6	3.7	21	0.11	HZ_sp unT	922	607	1,401
2008	42	199	99	1.49	2.3	1.7	3.1	16	0.01	HZ_sp	869	640	1,179
2009	42	197	72	1.67	1.6	1.0	2.3	20	0.05	HN_hp T250	595	400	886
2010	43	205	102	1.65	2.3	1.6	3.1	17	0.004	HN_cos	851	610	1,188

Mortality

Between 2006 and 2010, rangers found 100 dead roe deer, and most were found in late winter or early spring. The sex ratio was 0.9 ($n = 64$) and, although the sample size is small, apparently, the main causes of mortality were road accidents ($n = 10$) and drowning in canals ($n = 6$).

Biometrics

The average body masses of males and females were 23.6 kg (range 18-33, SD 2.7, $n = 115$) and 23.1 kg (range 17-31, SD 2.9, $n = 29$), respectively. The average longitudinal head-body lengths of males and females were 111.82 cm (range 95-126, SD 5.3) and 107 cm (range 91-121, SD 5.8), respectively. The average height at the withers of males and females was 70 cm (range 59-81, SD 5) and 68 cm (range 49-82, SD 5.3), respectively. On average, the chest perimeter of males and females was 68 cm (range 57-83, SD 4.7) and 65.5 cm (range 45-87, SD 8.9), respectively.

Hunting bags

The hunting quota was 208 males (from 183 hunts, or 88%) and 208 females (from 142 hunts, or 69). The actual bag was 45% of the quota (60% in males and 30% in females).

Discussion

The results of our study indicate that the estimates of the population densities of roe deer in the Aragon region of the Pyrenees based on Distance Sampling were at the low end of the range values reported for other Iberian and European populations. These densities can be considered low if we compare them with other studies in Spain (Martinez 1997; Burón *et al.*, 2005; Acevedo *et al.*, 2010). The densities in the Pyrenees seem to contrast with the observed values elsewhere in the Iberian Peninsula (see above) and elsewhere in Europe (Apollonio *et al.*, 2010).

Although some have argued against using the KAI to estimate population abundance because of its low reliability (Mayle *et al.*, 1999; Van Laere *et al.*, 1999), others have argued that it is useful for identifying

population trends, particularly, in Mediterranean regions (Acevedo *et al.*, 2008). Although the KAI has been used extensively to estimate the size of deer populations (Vincent *et al.*, 1991), line-transect sampling (DS) has become more common because the detection function can be estimated more easily (Thomas *et al.*, 2006). In large-scale studies, however, KAI estimates are commonly used to monitor and compare trends in populations, rather than to compare the densities of populations (Williams *et al.*, 2007).

In our study, the recovery of roe deer carcasses suggested that mortality was highest in late winter and early spring, which is the time of year when snow cover can hinder the animal's movements and its ability to find food, leaving it vulnerable to starvation (Myserud *et al.*, 1997) and predation (Jędrzejewska *et al.*, 1992). In addition, red fox is a potential predator of roe deer fawns (Panzacchi *et al.*, 2008) and roe deer mortality is a subject worthy of further study.

The balanced sex ratio observed reflects the proportion of the sexes in a population with a small level of extraction, which should be carefully monitored, given the difficulty of accomplishing the hunting quota. Our results suggest that there were slightly more females than males in the population; however, human harvesting may differ significantly from those derived from natural mortality (Solberg *et al.*, 2002). In our study area male roe deer are hunted preferentially because they have antlers. Since 2003, their populations have been managed to maintain high productivity, which allows high annual harvest rates. That management objective has been achieved by using sex-specific harvest quotas, with an emphasis on adult males, which we suspect has led to a low proportion of males in these populations. We recognize, however, that the observed sex ratio might not reflect the true population sex ratio because, in forest ecosystems, male roe deer are territorial between March and August, and pregnant females seek isolation in May before they give birth, and they rarely associate with others until August (Andersen *et al.*, 1998). Thus, males might be more easily detected than are females, and it is commonly assumed that estimates of sex ratios based on observations by hunters overestimate the proportion of males.

Roe deer density has become a topic of considerable interest. On one hand, some naturalists and tourists want high densities but, on the other hand, farmers and foresters prefer low or even zero densities (Meriggi *et al.*, 2009). Given the varying opinions, roe deer

management should strive for a balance between the various interests. In any case, a comprehensive understanding of the main parameters of population dynamics is a first step in developing the appropriate management of roe deer populations. Unfortunately, estimating roe deer densities is not a priority in European ungulate management and research. In a recent review of the status of wild ungulate populations in 29 European countries, only five countries provided data and had evaluated methods for estimating density (Apollonio *et al.*, 2010).

In our study, the fieldwork was a collaboration between the managers of hunting reserves and those that hunted in the Game Reserves, which was essential for the success of this monitoring programme, and we believe that this is a valid source of information in the study of mammals. The monitoring program was designed to include a representative sample of habitats, but it took into consideration the number and possible dedication of field personnel availability, basis of the long term monitoring. Our study demonstrated the potential of using various easily implemented methods that can be used by rangers and wildlife managers as useful and affordable tools for monitoring roe deer populations. Our results showed that collecting data for the calculation of indices of abundance is extremely important for the effective monitoring of populations. In our study, the collaboration of hunters and rangers facilitated the gathering of the data.

The roe deer population should continue to be monitored because long-term monitoring is required to assess the impact of management practices. Monitoring programs should include an assessment of deer abundance and their impacts on agriculture, forestry, and vegetation.

Acknowledgements

We thank the rangers who performed the fieldwork and the wildlife technicians of the regional government. The regional government financed the monitoring of the roe deer populations.

References

- Acevedo P, Delibes-Mateos M, Escudero MA, Vicente J, Marco J, Gortázar C, 2005. Environmental constraints in the colonization sequence of roe deer (*Capreolus capreolus* Linnaeus, 1758) across the Iberian Mountains, Spain. *J Biogeogr* 32: 1671-1680.
- Acevedo P, Ferreres J, Jaroso R, Durán M, Escudero MA, Marco J, Gortázar C, 2010. Estimating roe deer abundance from pellet group counts in Spain: an assessment of methods suitable for Mediterranean woodlands. *Ecol Indic* 10: 1226-1230.
- Acevedo P, Ruiz-Fons F, Vicente J, Reyes-García AR, Alzaga V, Gortázar C, 2008. Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. *J Zool* 276: 37-47.
- Acevedo P, Vicente J, Hofle U, Cassinello J, Ruiz-Fons F, Gortázar C, 2007. Estimation of European wild boar relative abundance and aggregation: a novel method in epidemiological risk assessment. *Epidemiol Infect* 135: 519-527.
- Andersen R, Duncan P, Linnell JDC, 1998. The European roe deer: the biology of success. Oslo: Scandinavian University Press.
- Apollonio M, Andersen R, Putman R, 2010. European ungulates and their management in the 21st Century. Cambridge University Press, Cambridge, UK.
- Buckland ST, Anderson DA, Burnham KP, Laake JL, 1993. Distance Sampling: estimating abundance of biological populations. Chapman & Hall, London, UK.
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L, 2001. Introduction to distance sampling. Oxford University Press, Oxford.
- Burón D, Fernández L, Martínez AL, López JC, Fernández-Mellado R, 2005. Status of roe deer population in Northern Guadalajara (Spain). Jerez.
- Cargnelutti B, Reby D, Desneux L, Angibault JM, Joachim J, AJM H, 2002. Space use by roe deer in a fragmented landscape. Some preliminary results. *Revue d'Ecologie (Terre Vie)* 57: 29-37.
- Focardi S, Aragno P, Montanaro P, Riga F, 2006. Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. *Ecography* 29: 407-417.
- Gill RMA, 1990. Monitoring the status of European and North American cervids. Nairobi: United Nations Environment Programme.
- Gordon IJ, Hester AJ, Festa-Bianchet M, 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *J Appl Ecol* 41: 1021-1031.
- Gortázar C, Herrero J, Villafuerte R, Marco J, 2000. Historical examination of the status of large mammals in Aragon, Spain. *Mammalia* 64: 411-422.
- Herrero J, 2003. Functional adaptation of wild boar to a forest ecosystem and an intensive agrarian ecosystem in Aragon. Publications of the Council for the Protection of Nature of Aragon. Investigation Series, 41.
- Jędrzejewska B, Jędrzejewski W, Bunevich AN, Milkowski L, Kasiński ZA, 1997. Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriol* 42: 399-451.

- Jędrzejewska B, Okarma H, Jędrzejewski WLM, 1994. Effects of exploitation and protection on forest structure, ungulate density and wolf predation in Białowieża Primeval Forest, Poland. *J Appl Ecol* 31: 664-676.
- Jędrzejewski W, Jędrzejewska B, Okarma H, Ruprecht AL, 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland. *Oecologia* 90: 27-36.
- Lerános I, Castián E, 1996. Evolución de la población del jabalí (*Sus scrofa* L., 1758) en Navarra (N Península Ibérica) (1996). *Misc Zool* 19: 133-139.
- Marco J, Herrero J, Escudero MA, Fernández-Arberas O, Ferreres J, García-Serrano A, Giménez-Anaya A, Labarta JL, Monrabal L, Prada C, 2011. Veinte años de seguimiento poblacional de ungulados silvestres en Aragón. *Pirineos* 166: 135-157.
- Martínez SJ, 1997. El corzo en la Reserva Regional de Caza de Ancares. *Veterinaria y Fauna Salvaje: Colegio Oficial de Veterinarios de Zamora*. pp: 91-110.
- Mayle BA, Peace AJ, Gill RMA, 1999. How many deer? A fieldguide to estimating deer populations. Edinburgh, Forestry Commission, UK.
- Meriggi A, Sotti F, Lamberti P, Gilio N, 2009. A review of the methods for monitoring roe deer European populations with particular reference to Italy. *Hystrix* 19: 103-120.
- Mysterud A, Bjornsen BH, Østbye E, 1997. Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway. *Wildl Biol* 3: 27-33.
- Osuna D, Prada C, Herrero J, Marco J, 2006-2008. Distribución de los ungulados silvestres en Aragón (2001-2005) determinada a partir de encuestas. *Lucas Mallada* 13: 191-212.
- Panzacchi M, Linnell JDC, Odden J, Odden M, Andersen R, 2008. When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. *Can J Zool* 86: 116-126.
- Prada C, Revilla M, García-Serrano A, Herrero J, Arnal MC, Martínez D, Fernández de Luco D, Pueyo JA, EE, 2007. Seguimiento y gestión del corzo *Capreolus capreolus* L. en las Reservas de Caza del Pirineo aragonés. Mieres, Asturias, Spain.
- Putman R, Watson P, Langbein J, 2011. Assessing deer densities and impacts at the appropriate level for management: a review of methodologies for use beyond the site scale. *Mammal Rev* 41: 197-219.
- Solberg EJ, Sæther B-E, Heim M, Ringsby TH, 2002. Biased adult sex ratio can affect fecundity in primiparous moose *Alces alces*. *Wildl Biol* 8: 117-128.
- Thomas L, Laake JL, Strindberg S, Marques FFC, Buckland ST, Borchers DL, Anderson DR, Burnham KP, Hedley SL, Pollard JH and others, 2006. Distance 5.0. Research Unit for Wildlife Population Assessment, University of St Andrews, UK.
- Thomas T, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP, 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J Appl Ecol* 47: 5-14.
- Van Laere G, Maillard J, Boutin M, Delome D, 1991. Le suivi des populations de chevreuils: des methodes traditionnelles d'estimation aux indicateurs population-environment. *Bulletin Mensuel de l'Office National de la Chasse* 244: 46-53.
- Vincent JP, Gaillard J-M, Bideau E, 1991. Kilometric index as biological indicator for monitoring forest roe deer populations. *Acta Theriol* 36: 315-328.
- Williams D, Acevedo P, Gortázar C, Escudero MA, Labarta JL, Marco J, Villafuerte R, 2007. Hunting for answers: rabbit (*Oryctolagus cuniculus*) population trends in northeastern Spain. *Eur J Wildlife Res* 53: 19-28.